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Evolution and Historical Biogeography of a Parasite-Host Assemblage: *Alcataenia* spp. (Cyclophyllidea: Dilepididae) in Alcidae (Charadriiformes)

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The methodology of phylogenetic systematics was used to develop hypotheses for the evolution of eight species of *Alcataenia*, a group of host-specific cestodes of the Alcidae and, to a lesser extent, the Laridae (Charadriiformes). Concurrently, aspects of the early biogeography of alcids were reevaluated making it possible to study the historical and distributional relationships of parasites and hosts. The most parsimonious hypothesis for the phylogeny of *Alcataenia* suggested that sequential colonization or host switching with limited coevolution (coaccommodation) by parasites best explained the distributional patterns exhibited by *Alcataenia* spp. Morphological evolution of specific species of *Alcataenia* accompanied host switching, but was limited subsequent to the initial event of colonization. Thus evolution of these parasites following colonization lagged behind continuing diversification of the host group. Although alcids are an ancient group, as indicated by palaeontological and phylogenetic data, their cestode fauna is apparently not. It is postulated that *Alcataenia* spp. were acquired by their characteristic hosts in the late Pliocene and early Pleistocene, following diversification of the Alcidae at the generic level during the Miocene. Host distributions of respective *Alcataenia* spp. are more narrow than expected, considering the relatively young age of this assemblage. The current paradigm linking pronounced host specificity with coevolution of hosts and parasites in assemblages of great evolutionary age is not supported.

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La méthodologie propre à la systématique phylogénétique a servi à élaborer des hypothèses sur l'évolution de huit espèces d'*Alcataenia*, un groupe de cestodes spécifiques aux Alcidae et, à un degré moindre, aux Laridae (Charadriiformes). En outre, certains aspects de la biogéographie primitive des alcidés ont été réexaminés de façon à permettre l'étude des relations historiques et géographiques des parasites et des hôtes. L'hypothèse la plus simple sur la phylogénie d'*Alcataenia* suggère que la colonisation séquentielle, ou changement d'hôte par les parasites et coévolution limitée (coaccomodation), est le phénomène qui peut le mieux expliquer la répartition actuelle des espèces d'*Alcataenia*. Certaines espèces particulières d'*Alcataenia* ont subi une évolution morphologique en changeant d'hôte, mais cette évolution a été ralentie après le début de la colonisation. L'évolution de ces parasites après la colonisation a donc pris du retard par rapport à la diversification continue du groupe hôte. Bien que les Alcidae constituent un groupe ancien, d'après les données paléontologiques et phylogénétiques, la faune de cestodes qui les parasite ne semble pas l'être. Il semble que les diverses espèces d'*Alcataenia* soient devenues les parasites de leurs hôtes respectifs vers la fin du Pliocène et le début du Pleistocène, à la suite de la diversification des Alcidae au niveau générique au cours du Miocène. La répartition chez les hôtes des diverses espèces d'*Alcataenia* n'est pas aussi répandue que pourrait le laisser croire l'existence relativement récente de ces associations. Cette étude ne confirme pas le paradigme généralement accepté selon lequel une grande spécificité d'hôte est reliée à la coévolution des hôtes et des parasites dans les associations très anciennes.
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Introduction

Coevolution of parasite–host assemblages is a widely recognized concept (Brooks 1979*a*; Mitter and Brooks 1983; and others). There have been relatively few studies objectively assessing the extent and significance of this phenomenon (Brooks 1977, 1978, 1979*a*, 1979*b*; Brooks *et al.* 1981; Platt 1984; Glen and Brooks 1985) and none have dealt with cyclophyllidean cestodes in avian hosts. Krabbe (1869) and Fuhrmann (1908) were among the first to critically recognize that specific taxa of cestodes were often characteristic of limited and phylogenetically related taxa of birds. The analysis reported here is the first attempt to develop hypotheses for the evolution and historical biogeography of *Alcataenia* spp. (Dilepidinae Fuhrmann, 1907) and their charadriiform hosts.

The principle hosts for *Alcataenia* spp., seabirds of the family Alcidae, represent a monophyletic assemblage of genera and species of great evolutionary age (Kozlova 1957; Storer 1960; Udvardy 1963; Olson 1985; Strauch 1985; and others). The family contains 23 Recent species distributed among 12 genera: puffins include two genera and four species (*Cerorhinca monocerata* (Pallas), *Fratercula cirrhata* (Pallas), *F. arctica* (Linnaeus), and *F. corniculata* (Naumann)); auklets comprise three genera and five species (*Ptychoramphus aleuticus* (Pallas), *Cyclorrhynchus psittacula* (Pallas), *Aethia cristatella* (Pallas), *A. pusilla* (Pallas), and *A. pygmaea* (Gmelin)); murrelets are represented by two genera and six species (*Brachyramphus marmoratus* (Gmelin), *B. brevirostris* (Vigors), *Synthliboramphus antiquus* (Gmelin), *S. wumizuzume* (Temminck), *S. craveri* (Salvadori), and *S. hypoleucus* (Xántus de Vesey)); guillemots are monogeneric with three species (*Cepphus carbo* Pallas, *C. columba* Pallas, and *C. grylle* (Linnaeus)); dovkies are monotypic (*Alle alle* (Linnaeus)); and the auks include the murres (*Uria aalge* (Pontoppidan), *U. lomvia* (Linnaeus)), razorbills (*Alca torda* Linnaeus), and the recently extinct great auk (*Pinguinus impennis* (Linnaeus)). The family is restricted to high latitudes in the northern hemisphere, and most taxa are endemic to either the Pacific basin (16 species) or the Atlantic basin (3 species, including the great auk). Only four genera and four species have distributions that are circumpolar (Udvardy 1963, 1979). Most members of the family have ranges centred in the region of the Bering Sea, including the Aleutian Islands, islands of the Bering Sea, and some areas of the surrounding coasts (for range maps, see Storer 1952; Udvardy 1963; Kozlova 1957). Consequently, the centre of origin for the family is considered to be the north Pacific (Udvardy 1963; Olson 1985). Several works have dealt with biogeography and evolution

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within the family (Kaftanovskii 1951; Storer 1945*a*, 1945*b*, 1952, 1960; Kozlova 1957; Udvardy 1963; Bédard 1969). Recent advances in interpretation of the phylogenetic (Strauch 1985) and palaeontological (Olson 1985) relationships of the family have made it necessary to reevaluate the historical biogeography of the alcids. New hypotheses for the distributional history of alcids are presented in the current study.

In the Holarctic, species of *Alcataenia* Spasskaya, 1971 are host-specific parasites of the Alcidae and, to a lesser extent, the Larinae (Charadriiformes) (Spasskaya 1971; Hoberg 1984*a*, 1984*b*). The genus contains seven species in alcids: *Alcataenia campylacantha* (Krabbe, 1869) (type) in species of *Cepphus* Pallas; *A. armillaris* (Rudolphi, 1810), *A. meinertzhageni* (Baer, 1956), and *A. longicervica* Hoberg, 1984 in the species of *Uria* Brisson; *A. pygmaeus* Hoberg, 1984 in *Aethia pygmaea*; *A. fraterculae* Hoberg, 1984 in *Fratercula corniculata*; and *A. cerorhincae* Hoberg, 1984 in *Cerorhinca monocerata*; and three species in larids: *A. larina* (Krabbe, 1869), *A. micracantha* (Krabbe, 1869), and *A. dominicanus* (Railliet and Henry, 1912) (Hoberg 1984*b*, 1984*c*, 1984*d*, 1984*e*). The limits on the latter two species have yet to be clearly defined (Joyeux and Baer 1954; Matevosian 1963; Spasskii 1968; Odening 1982; Zdzitowiecki and Szelenbaum-Cielecka 1984); consequently they are excluded from further consideration. Additional species of *Alcataenia* may be represented in murrelets of the genus *Brachyramphus* Brandt and possibly in *Alle alle* (Threlfall 1971; Hoberg 1984*e*). Characteristic cestodes are unknown from *Alca torda, Fratercula cirrhata, Fratercula arctica, Aethia pusilla,* and *A. cristatella* although adequate samples have been examined of these species. Insufficient specimens of *Pinguinus impennis*, all species of *Synthliboramphus* Brandt, *Ptychoramphus aleuticus,* and *Cyclorrhynchus psittacula* have been collected to assess the presence or absence of specific *Alcataenia* spp. in these seabirds (Hoberg 1984*a*).

In previous studies of *Alcataenia* spp. in alcids and larids, patterns of host–parasite colonization and coevolution were suggested by (*i*) congruent geographical distributions of hosts and parasites, (*ii*) morphology of particular species of *Alcataenia*, and (*iii*) historical biogeographical relationships of the host group (Hoberg 1984*a*, 1984*c*, 1984*d*). However, the temporal aspects of these relationships and the phylogenetic linkages among species occurring in puffins, auklets, murres, and guillemots were unknown. Thus the relative contribution of coevolution versus colonization in development of this assemblage could not be substantiated (see Brooks 1979*a*). In the present study, results of an analysis of eight species of *Alcataenia*, using phylogenetic systematics (Hennig 1966; Wiley 1981), in conjunction with a reevaluation of historical biogeography, employing new data about the palaeontology (Olson 1985) and phylogeny of alcids (Strauch 1985), were used to develop robust hypotheses for the evolution of this parasite–host assemblage.

Materials and methods

The relationships of eight species and two subspecies of *Alcataenia* were analyzed using cladistics or phylogenetic systematics (Hennig 1966; Wiley 1981). Detailed summaries of this methodology have been presented by Brooks and co-workers (Brooks *et al.* 1984; Brooks *et al.* 1985*a*; Glen and Brooks 1985). The PHYSYS computer systematics system (developed by Dr. J. S. Farris, State University of New York, Stony Brook, and Mary F. Mickevich) was used as an aid in the analysis.

Although ten nominal species and subspecies are recognized in *Alcataenia* (see Hoberg 1984*e*), only eight species were considered in the study. The following were included in the ingroup: *Alcataenia campylacantha, A. armillaris, A. meinertzhageni, A. longicervica, A. pygmaeus, A. fraterculae, A. cerorhincae,* and *A. larina* (with *A. l. larina* and *A. l. pacifica* considered as distinct). Two species, *A. micracantha* and *A. dominicanus* were excluded because of uncertain taxonomic relationships, particularly with reference to other nominal taxa that have been suppressed as their synonyms (see Joyeux and Baer 1954; Odening 1982; Zdzitoweicki and Szelenbaum-Cielecka 1984).

Specimens of all *Alcataenia* spp. and representatives of several prominent genera of the Dilepidinae were examined. A detailed listing of specimens of *A. campylacantha, A. armillaris, A. meinertzhageni, A. pygmaeus, A. fraterculae, A. cerorhincae, A. longicervica,* and *A. larina* can be found elsewhere (Hoberg 1984*b*, 1984*c*, 1984*d*, 1984*e*). Others were borrowed from the Museum d'Histoire Naturelle, Génève (MHN), the U.S. National Museum (USNM), and the collections of Robert L. Rausch (RLR) or are maintained in the author's collections (EPH). Additional specimens included: *Alcataenia micracantha* (MHN-84/69–89, 107/93–99, and 122/48; EPH-392, 396, 130, 142); *Alcataenia dominicanus* (MHN-110/66–72; EPH-1764, 1770); *Anomotaenia microrhyncha* (Krabbe, 1869) (MHN-42/23–30, 113/10–12, 113/22–23, 27/47–49, 114/1); *Choanotaenia infundibulum* (Bloch, 1779) (USNM-40350, 41606, 46707); *Dictymetra paranumenii* Clark, 1952 (RLR—); and *Paricterotaenia porosa* (Rudolphi, 1810) (RLR-15120).

Character analysis

Characters employed in the analysis were derived from a study of *Alcataenia* spp. and some related dilepidids, along with reference to recent descriptions and redescriptions (Hoberg 1984*b*, 1984*c*, 1984*d*, 1984*e*), monographs on the Dilepididae (Matevosian 1963; Spasskaya and Spasskii 1977, 1978), and treatments of other cestodes (Fuhrmann 1932; Wardle and McLeod 1952; Yamaguti 1959; Schmidt 1986). Polarization of character state transformation, i.e., determination of primitive (plesiomorphic) versus derived (apomorphic) condition (Hennig 1966; Wiley 1981), was accomplished by outgroup comparison (Lundberg 1972; Wiley 1981). The primary outgroup was the genus *Anomotaenia* Cohn, 1900. This genus was selected on the basis of its morphological similarity to *Alcataenia* and its occurrence in more primitive charadriiforms (scolopacids) (Sibley and Ahlquist 1986; Olson 1985).

The polarity of transformation series for two characters, length of rostellar hooks and structure of the genital atrium, could not be reliably determined with reference to the taxonomic outgroup. Consequently the functional outgroup, the most plesiomorphic members of *Alcataenia*, was used to determine the direction of these homologous series (Watrous and Wheeler 1981; Glen and Brooks 1985). Additionally, one character, position of genital ducts, was split into two independent transformation series because of the way data sets are read by PHYSYS (see Glen and Brooks 1985). A summary of the 20 characters, representing 16 homologous series, used in the analysis is presented below and in a numerically coded matrix (Table 1). Plesiomorphic states of characters are designated as 0, apomorphic as 1 or 2.

1. Genital atrium: The atrium is weakly muscular and not prominent in *Anomotaenia*. Among *Alcataenia* it is generally papillalike or strongly muscular. Three states: weakly developed (0); papillalike (1); muscular (2).
2. Uterus: The uterus is reticulate in *Anomotaenia* and *Alcataenia*; however, ontogeny and structure differ markedly. Two states: thin-walled, narrow, multi-layered (0); flat, broad, single-layered, development by posteriad extension (1).

3,4. Position of genital ducts: This character was split into two separate transformation series (see Glen and Brooks 1985). In *Anomotaenia* the genital ducts pass between the poral excretory canals, while in *Alcataenia* they are between (0,0) or dorsal to (0,1) the canals, or variable (1,0) in position. Character 3: Two states: between (0); variable (1). Character 4: Two states: between (0); dorsal (1).

5. Wall of vagina: Species of *Anomotaenia* typically have thin-walled vaginas, while in *Alcataenia* they may be markedly thickened. Two states: thin (0); thick (1).

TABLE 1. Character matrix for *Alcataenia* spp.

	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. campylacantha	1	1	0	0	1	2	0	1	0	1	1	0	0	1	0	0
A. armillaris	1	1	0	1	1	1	1	0	0	1	1	1	1	0	0	0
A. meinertzhageni	1	1	0	0	1	2	1	1	0	2	1	0	0	1	1	1
A. longicervica	1	1	0	1	1	1	1	0	0	1	1	2	0	1	1	1
A. pygmaeus	2	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0
A. fraterculae	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
A. cerorhincae	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
A. larina larina	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
A. larina pacifica	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0

6. Length of rostellar hooks: Among species of *Alcataenia* there are forms with large (>80 μm), medium (~40 μm), and small (<30 μm) hooks. Three states: large (0); medium (1); small (2). Because of variation in the length of hooks in the primary outgroup and others, the functional outgroup method was used to determine polarization (Watrous and Wheeler 1981; Glen and Brooks 1985).
7. Position in host intestine: Species of *Anomotaenia* are only superficially attached to the host mucosa. Specimens of *Alcataenia* spp. are either superficially attached or deeply embedded in the host mucosa. Two states: superficial (0); embedded (1).
8. Wall of cirrus sac: The wall of the cirrus sac is either thin or thick and highly muscular. Two states: thin (0); thick (1).
9. Sphincter on seminal receptacle: A prominent sphincter located proximally on the seminal receptacle is absent in *Anomotaenia* and most *Alcataenia*. Two states: absent (0); present (1).
10. Distribution of rostellar hooks: In all species of *Anomotaenia* hooks are distributed in two regularly alternating rows, with equal numbers in the anterior and posterior. Among *Alcataenia* spp. hooks are distributed in two rows but alternation may be regular, irregular, or a mosaic. Three states: regular (0); irregular (1); mosaic (2).
11. Ovary: In *Anomotaenia* and some *Alcataenia* the ovary is highly lobed. In other *Alcataenia* spp. the ovary is initially reticulate and later lobed. Two states: lobed (0); initially reticulate (1).
12. Length of neck: Species of *Anomotaenia* are generally characterized by short necks. Species of *Alcataenia* exhibit short (≤400 μm), intermediate (≥800 μm), and long (>1000 μm) necks. Three states: short (0); intermediate (1); long (2).
13. Shape of proglottid: In *Anomotaenia* and most *Alcataenia* mature and gravid proglottids are typically wider than long. Only in *A. armillaris* are they longer than wide. Two states: wide (0); long (1).
14. Length of cirrus sac: Among *Anomotaenia* the cirrus sac is relatively long, i.e., crosses the poral osmoregulatory canals. In *Alcataenia* this organ is either long or short, i.e., attaining but not substantially crossing the canals. Two states: long (0); short (1).
15. Position of testes: Among *Anomotaenia* the testes are entirely posterior to the female organs. In *Alcataenia* they are primarily posterior, but in some species may attain a position lateral to the female organs in the antiporal half of the segment. Two states: posterior (0); lateral (1).
16. Position of female organs: The Mehlis' gland and vitelline gland are median among *Anomotaenia* spp. In *Alcataenia* these organs may lie in the poral half of the proglottid. Two states: median (0); poral (1).

The consistency index (CI), a measure of the fit of specific characters to a hypothetical phylogeny, was also determined (Farris 1970). This value is calculated by dividing the minimum numbers of steps required to represent the data by the actual number of changes needed to describe a given phylogenetic tree. The CI is a measure of how well a given data set describes a particular tree; i.e., a CI of 1.0 suggests a lack of homoplasy in a given character or set of characters.

Results

Phylogenetic hypotheses were developed for the relationships of eight species of *Alcataenia*. Two cladograms, differing slightly in topology of terminal taxa, resulted from the analysis of 16 homologous series representing 20 characters. The most parsimonious statement, with a CI of 77%, for the phylogeny of *Alcataenia* is shown in Fig. 1. This overall CI is high, and indicates a good fit of the data to the tree. Consistency values for individual characters are given in Table 2. Homoplasy resulting from parallel development in four characters is postulated (wall of cirrus sac, length of neck, position of testes, and position of female organs). Two characters were influenced by evolutionary reversals (position of genital ducts and position in host mucosa).

The monophyletic nature of *Alcataenia* is supported by two characters: structure of the genital atrium, and ontogeny and structure of the uterus. The most plesiomorphic species (*Alcataenia larina*, represented by *A. l. pacifica* and *A. l. larina; A. fraterculae;* and *A. cerorhincae)* form a morphologically uniform group. The relationship of *A. l. larina* and *A. fraterculae* is unresolved based on this analysis. However, these latter taxa are clearly distinguished by morphological characters not amenable to cladistic analysis (absolute measurements of rostellar hooks, cirrus sac, and vitelline gland; and number of testes) (Hoberg 1984*c*). The remaining species, *A. pygameus, A. armillaris, A. longicervica, A. meinertzhageni,* and *A. campylacantha*, are characterized by a greater degree of morphological differentiation. Homoplasy and reversals are postulated only among characters that distinguish these latter species of cestodes (Fig. 1 and Table 2).

Discussion

The host and geographic ranges of parasites are historically constrained by evolution and ecological associations (Brooks 1979*a*, 1981, 1985). Consequently, the interpretation of the evolutionary history of a specific group of helminths must be taken in context with that of its hosts. The development of hypotheses about the evolution of an assemblage is dependent upon knowledge of host phylogeny, chronology of the fossil record, and historical biogeography.

Individual species of *Alcataenia* are highly host specific and are typically limited to a single genus or species among the Alcidae (Table 3). Geographical ranges of *Alcataenia* spp. may be narrow or broad, and are largely congruent with those of their

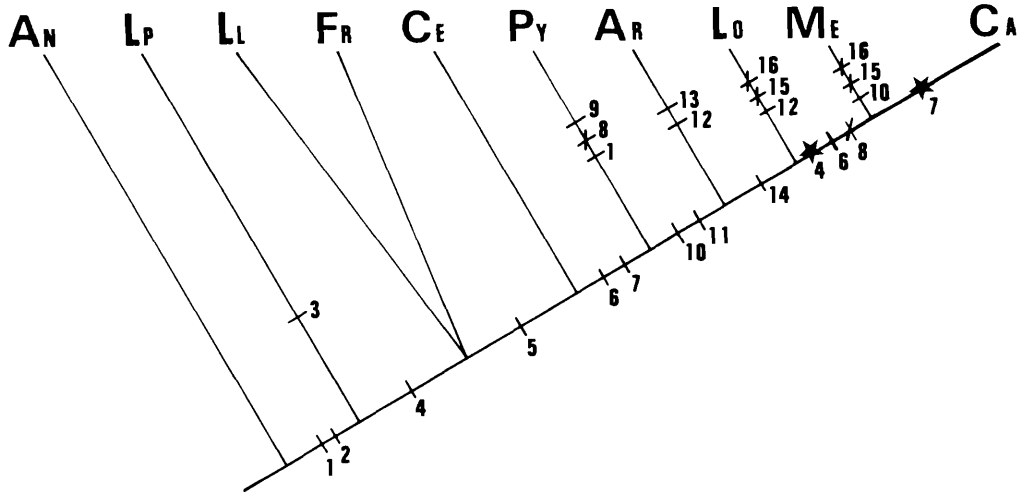


FIG. 1. Cladogram depicting hypothesis for the evolution of *Alcataenia* spp. This tree is the most parsimonious representation of 16 morphological characters. Taxa are as follows: AN, *Anomotaenia* (outgroup); LP, *A. larina pacifica*; LL, *A. l. larina*; FR, *A. fraterculae*; CE, *A. cerorhincae*; PY, *A. pygamaeus*; AR, *A. armillaris*; LO, *A. longicervica*; ME, *A. meinertzhageni*; and CA, *A. campylacantha*. Refer to diagnoses in text for identity of individual characters. ★, evolutionary reversals; ×, postulated homoplasy.

TABLE 2. Consistency indices (CI) for characters used in analysis of *Alcataenia*

Character No.	Character	CI
1	Genital atrium	100.00
2	Uterus	100.00
3	Genital ducts	100.00
4	Genital ducts	50.00
5	Vagina	100.00
6	Hooks: size	100.00
7	Position in host	50.00
8	Cirrus sac	50.00
9	Seminal receptacle	100.00
10	Hooks: position	100.00
11	Ovary	100.00
12	Neck	66.66
13	Proglottid	100.00
14	Cirrus sac: length	100.00
15	Testes	50.00
16	Female organs	50.00

hosts (Figs. 2–7; Table 3). Although murrelets of the genera *Brachyramphus* and *Synthliboramphus* and the auklets *Ptychoramphus aleuticus* and *Cyclorrhynchus psittacula* have not been adequately examined, definable relationships are evident among other alcids and *Alcataenia* spp. In previous studies, patterns of host–parasite colonization and coevolution were suggested by (*i*) congruent geographic distributions of hosts and parasites, (*ii*) morphology of particular *Alcataenia* spp., and (*iii*) historical biogeographical relationships of the Alcidae (Hoberg 1984*a*, 1984*c*, 1984*d*). However, clear phylogenetic hypotheses were not available for parasites or hosts (Hoberg 1984*a*).

Phylogeny of the Alcidae

The sister group for the Alcidae appears to be the Lari (Storer 1960; Strauch 1985). Among the alcids, the puffins, auklets, and auks have generally been recognized as natural groups (Kozlova 1957; Storer 1960). The phylogenetic relationships of these, and the status of the murrelets, guillemots, and dovekies, have remained enigmatic. The long evolutionary history of the family (many extant genera known from the late Miocene) has obscured its origins and complicated attempts at phylogenetic reconstructions (Olson 1985; Strauch 1985).

Strauch (1985) employed character compatibility analysis to develop hypotheses for the phylogeny of Recent genera of alcids (Fig. 8). Puffins (*Cerorhinca, Lunda,* and *Fratercula*) appear to be the sister group for the remaining taxa of modern alcids. The auklets (*Ptychoramphus, Cyclorrhynchus,* and *Aethia*) are recognized as a monophyletic assemblage directly related to the puffins. The relationships of the murrelets and guillemots are unresolved, although *Brachyramphus* is apparently not close to *Synthliboramphus* and *Cepphus*, while the latter two may be sister taxa. *Alle* is considered distinct from the auks (*Uria, Alca,* and *Pinguinus*). The murres and remaining auks, the most highly derived alcids, apparently shared a common ancestor. In the context of the present study it is notable that (*i*) puffins are the most primitive alcids, and *Fratercula* spp. are derived within the assemblage sharing a common ancestor with *Cerorhinca*; (*ii*) *Aethia* spp. are the most highly derived auklets; and (*iii*) *Cepphus* is more closely related to *Synthliboramphus* than to *Uria* and the auks.

The family Alcidae is a phylogenetically old group represented by an array of extinct and Recent genera and species distributed in the oceans of the northern hemisphere. The origin of the group was probably in the Palaeocene, although the earliest known fossil currently thought to be an alcid is of Eocene age (Storer 1960; Olson 1985). Alcids initially developed in the Pacific basin and only later entered the Atlantic (Kozlova 1957; Udvardy 1963; Olson 1985). By late Miocene and early Pliocene, representatives of many extant genera, including puffins (*Cerorhinca* spp.), auklets (*Ptychoramphus* and *Aethia*), murrelets (*Brachyramphus* and *Endomychura* Oberholser), guillemots (*Cepphus*), and murres (*Uria*), were known from the eastern North Pacific. The late Tertiary alcids of the Atlantic were represented by *Miocepphus* Wetmore, *Australca* Brodkorb (an indeterminant number of species), possibly *Alle* Link, *Pinguinus* Bonnaterre, *Alca* Linnaeus, and *Fratercula* (Olson 1985). Alcids were distributed in two allopatric centres of abundance through the later Tertiary. Endemism of the puffin–auklet, murrelet–guillemot, and murre assemblage of the Pacific and the auks of the Atlantic indicates a lack of interchange between

TABLE 3. Host distribution for *Alcataenia* spp. in Alcidae

Host*	Parasite	Geographical range
Tribe Fraterculinae		
Cerorhinca monocerta	*A. cerorhincae*	Pacific basin
Fratercula cirrhata	None	—
Fratercula arctica	None	—
Fratercula corniculata	*A. fraterculae*	Pacific basin
Tribe Aethiini		
Ptychoramphus aleuticus	†	—
Cyclorrhynchus psittacula	†	—
Aethia pusilla	None	—
Aethia pygmaea	*A. pygmaeus*	Central Aleutian Islands
Aethia cristatella	None	—
Tribe Brachyramphini		
Brachyramphus brevirostris	*Alcataenia* sp.‡	Pacific basin
Brachyramphus marmoratus	†	—
Tribe Cephphini		
Cepphus carbo	*A. campylacantha*	Holarctic
Cepphus columba	*A. campylacantha*	Holarctic
Cepphus grylle	*A. campylacantha*	Holarctic
Synthliboramphus hypoleucus	†	—
Synthliboramphus craveri	†	—
Synthliboramphus antiquus	†	—
Synthliboramphus wumizuzume	†	—
Tribe Alcini		
Alle alle	§	—
Uria aalge and *Uria lomvia*	*A. armillaris*	Holarctic
	A. longicervica	Pacific basin
	A. meinertzhageni	Holarctic
Alca torda	None‖	—
Pinguinus impennis	†	—

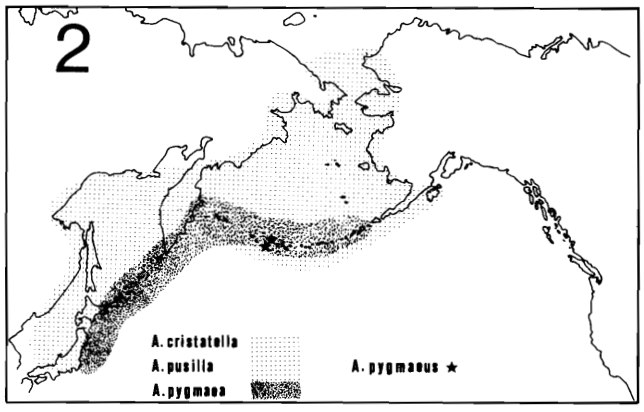
*Host list in phylogenetic order, modified from Strauch (1985).
†Insufficient numbers of specimens examined to determine presence or absence of *Alcataenia* spp.
‡*Alcataenia* sp. indet., described by Hoberg (1984*e*).
§*Anomotaenia* sp. (? = *Alcataenia* sp.) was reported by Threlfall (1971).
‖*Alcataenia armillaris* is known from *Alca torda*, but this alcid does not appear to be a typical host for this cestode (reviewed by Hoberg 1984*a*).

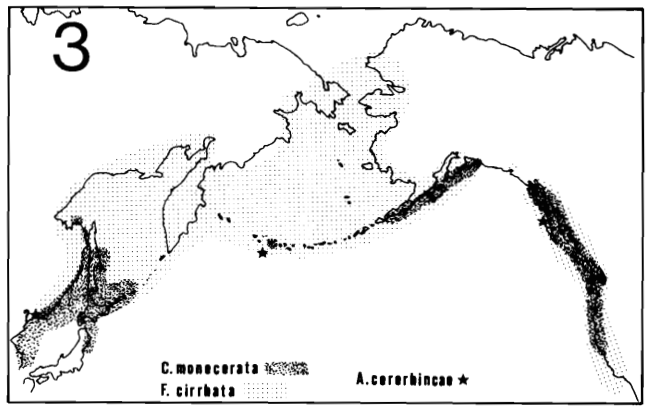
the faunas. Puffins are the only Tertiary–Pacific alcids represented in the Atlantic while there are no good records indicating dispersal from the Atlantic to the Pacific before the Quaternary (Olson 1985).

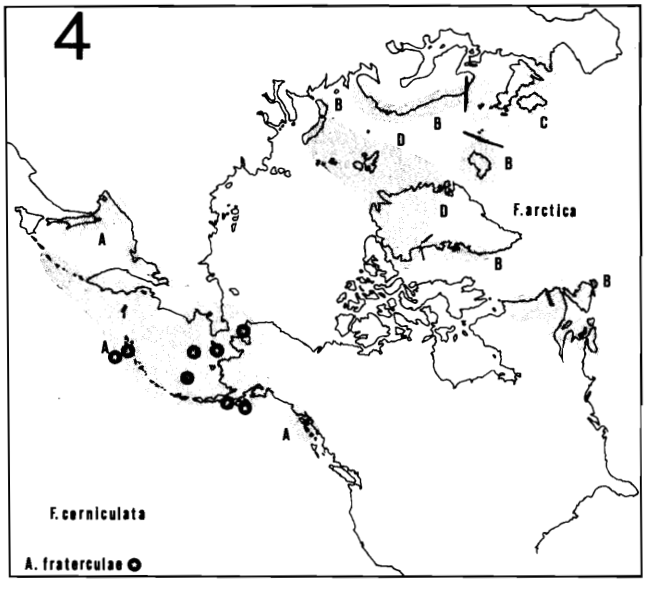
Parasite–host relationships

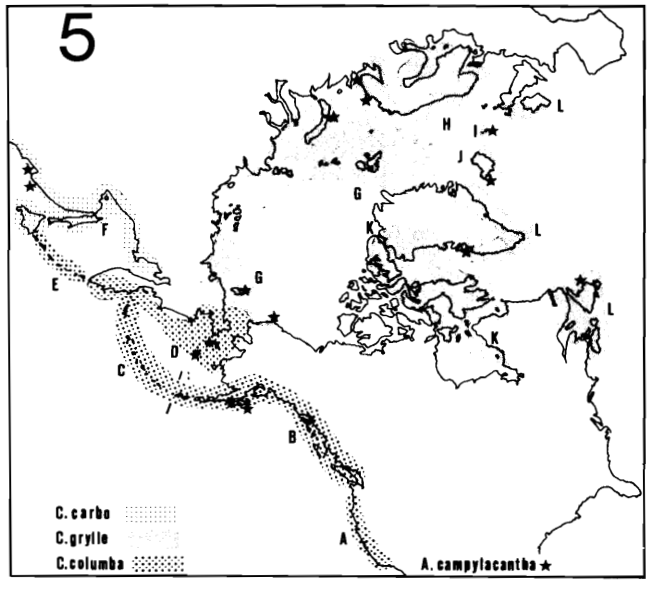
The distribution of helminths in hosts can be explained by either historical coevolutionary or ecological factors. Long-term phylogenetic relationships between hosts and parasites are indicative of coevolution (cospeciation and coaccommodation) within an assemblage (Brooks 1979*a*). Other distributional patterns may have resulted from successful colonization or transfer of parasites between hosts that are ecologically similar. There may be two results of colonization: the parasite may speciate or remain as an opportunistic component of the helminth fauna of its new host. In situations of cospeciation or narrow coaccommodation, accompanied by the development of host specificity, parasites can be used as direct indicators of host phylogeny (Brooks 1979*a*, 1981; Brooks *et al.* 1981). In hosts with complex geographic distributions, parasites may then be used to study historical relationships and the relative stability of a fauna through time. Widespread allopatric distributions of

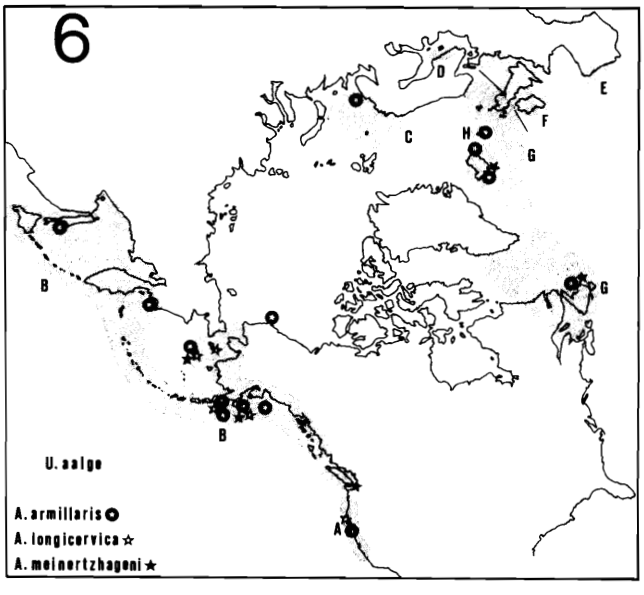
FIGS. 2–7. Approximate breeding distribution for some alcids, and minimum geographical ranges of *Alcataenia* spp. as determined by collections. Fig. 2. Distribution of *Aethia* spp. and *A. pygmaeus* in *Aethia pygmaea* (see Hoberg 1984*b*). Fig. 3. Distribution of *Cerorhinca monocerata* and *Fratercula cirrhata*. Range of *A. cerorhincae* in *C. monocerata* (Hoberg 1984*c*). Fig. 4. Distribution of *Fratercula corniculata* (A) and *F. arctica* including *F. arctica arctica* (B), *F. a. grabae* (C), and *F. a. naumanni* (D). Range of *A. fraterculae* in *F. corniculata* (Hoberg 1984*c*). Fig. 5. Distribution of *Cepphus columba* including *C. c. eureka* (A); *C. c. adianta* (B); *C. c. kaiurka* (C); *C. c. columba* (D); and *C. c. snowi* (E). Distribution of *C. carbo* (F); and *C. grylle* including *C. g. mandtii* (G); *C. g. grylle* (H); *C. g. faeroeensis* (I); *C. g. islandicus* (J); *C. g. ultimus* (K), and *C. g. arcticus* (L). Range of *A. campylacantha* (Hoberg 1984*e*). Fig. 6. Distribution of *Uria aalge* including *U. a. californica* (A); *U. a. inornata* (B); *U. a. hyperborea* (C); *U. a. intermedia* (D); *U. a. ibericus* (E); *U. a. albionis* (F); *U. a. aalge* (G); and *U. a. spiloptera* (H). Range of *A. armillaris*, *A. longicervica*, and *A. meinertzhageni* in *U. aalge* (Hoberg 1984*d*). Fig. 7. Distribution of *U. lomvia* including *U. l. arra* (A); *U. l. heckeri* (B); *U. l. eleonorae* (C); *U. l. arroides* (D); and *U. l. lomvia* (E). Range of *A. armillaris*, *A. longicervica*, and *A. meinertzhageni* in *U. lomvia* (Hoberg 1984*d*). Distribution of alcids from Salomonsen (1944), Storer (1952), Kozlova (1957), Tuck (1960), Udvardy (1963, 1979), and Sowls *et al.* (1978).

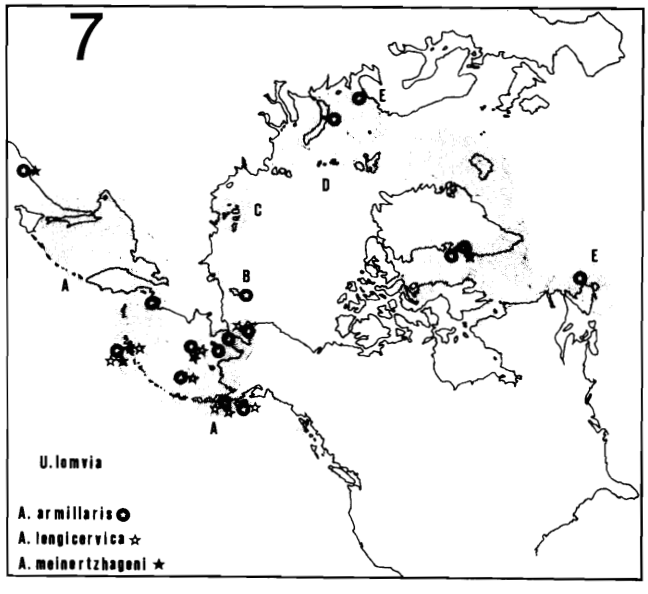

2
A. cristatella
A. pusilla
A. pygmaea
A. pygmaeus ★


3
C. monacorata
F. cirrhata
A. cererbincae ★


4
F. arctica
F. corniculata
A. fraterculae ⊙


5
C. carbo
C. gryllo
C. columba
A. campylacantha ★


6
U. aalge
A. armillaris ⊙
A. longicervica ☆
A. meinertzhageni ★


7
U. lomvia
A. armillaris ⊙
A. longicervica ☆
A. meinertzhageni ★

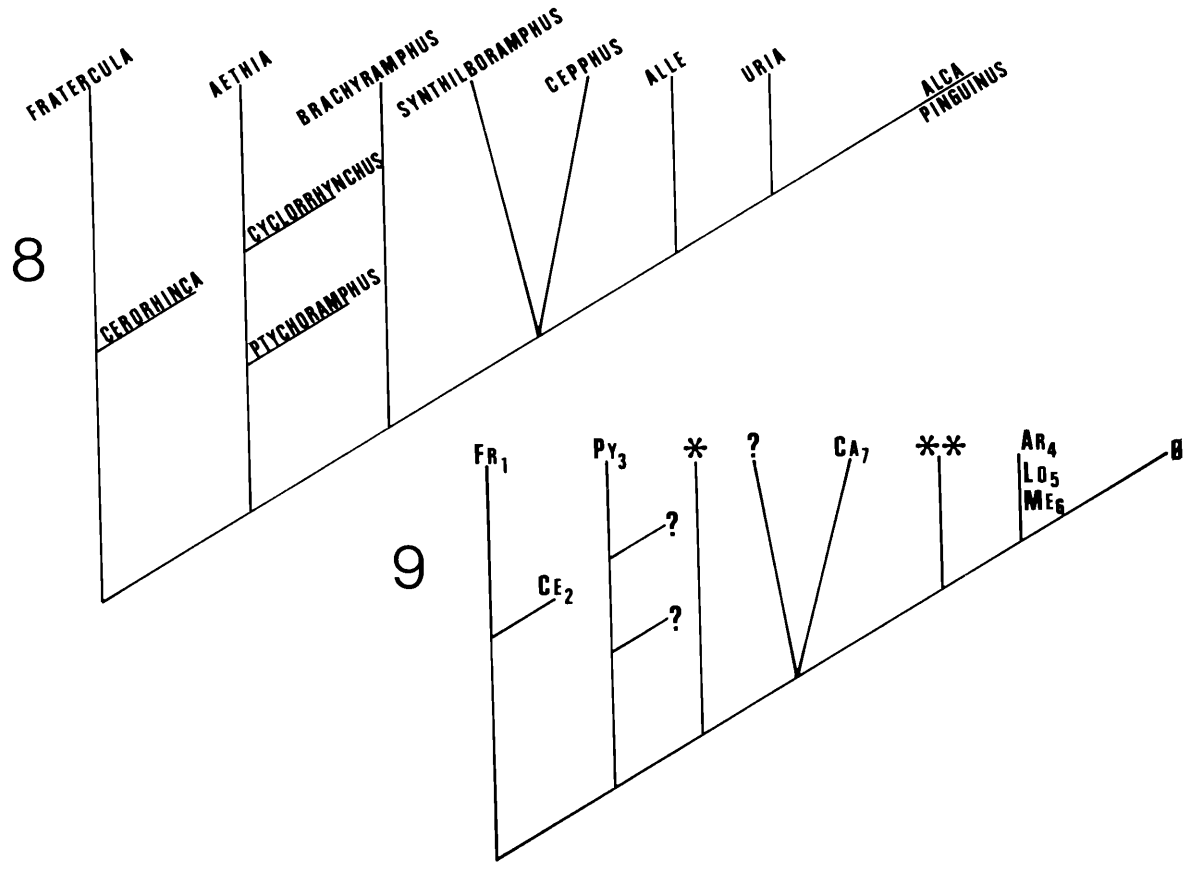


FIG. 8. Cladogram for the Alcidae derived from Strauch (1985). FIG. 9. Host cladogram depicting incongruent distribution of *Alcataenia* in the Alcidae, indicative of colonization. Subscripts denote sequence of evolution of *Alcataenia* spp.; *, *Alcataenia* sp. indet. described by Hoberg (1984*e*); **, *Anomotaenia* sp. (= *Alcataenia*?) reported by Threlfall (1971); ?, insufficient specimens examined to determine presence or absence of parasites; $\emptyset$, species of *Alcataenia* unknown. Other abbreviations are defined in caption for Fig. 1.

host-specific assemblages of parasites which have heteroxenous life cycles may indicate the relative stability of past environments and yield important information about the evolution of ecological associations.

Host specificity refers to the phenomenon in which species of helminths are limited in distribution to phylogenetically related hosts. Generally, some degree of long-term coevolution is implied between host and parasite (Mayr 1957), although the age of most associations is unknown. Specificity as exhibited by dilepidid cestodes of the Alcidae (those in puffins, auklets, guillemots and murres) is indicated by complete development (egg production) being limited to a narrow range of related hosts (generally congeners) (Hoberg 1984*a*). This observation is compatible with the assertion of Rausch (1983) that specificity can be represented by a "positive–negative dichotomy." Data concerning parasites of alcids do not support the contention by Dogiel (1964), Holmes *et al.* (1977), and Holmes (1979) that specificity is a continuum over a range of preferred to nonpreferred hosts. The patterns observed are ones of presence and absence, rather than a broad host distribution. Development to maturity and successful reproduction are limited to a single species of host or to small, phylogenetically related groups.

Distributions of geographically widespread parasites, such as some *Alcataenia* spp., that are also host specific indicate that similar biotic conditions (the capability of completing life cycles) existed during the dispersal or speciation of the host group. This is particularly the case (and also most instructive) where several species or subspecies of hosts that have allopatric distributions and continue to be isolated share a single species or several related species of host-specific parasites.

Parasite–host evolution and biogeography

Sequential colonization or host switching with limited coevolution (predominately coaccommodation) (see Brooks 1979*a*) by parasites best explains the distributional patterns exhibited by *Alcataenia* spp. Current hypotheses for the phylogeny of alcids, their broader relationships within Charadriiformes, and that of *Alcataenia* spp. are not compatible with a coevolutionary history for hosts and parasites. These patterns are best illustrated by demonstrating the incongruence of parasite and host cladograms (Figs. 1, 8–10).

Anomotaenia or another similar dilepidid of terrestrial origin is the probable sister group of *Alcataenia*. The primary hosts of *Anomotaenia* are Scolopacidae (Spasskaya and Spasskii, 1978), shorebirds that are phylogenetically older than but not directly related to the Laridae and Alcidae (Olson 1985; Sibley and Ahlquist 1986). These relationships and the limited occurrence of *Alcataenia* spp. in larids (Hoberg 1984*a*) is compatible with a host distribution resulting from colonization of gulls by a proto-*Alcataenia* from shorebirds. It is postulated that development of *Alcataenia* in larids proceeded first in freshwater–estuarine environments and only later was there colonization of pelagic hosts in marine habitats. Although larids and alcids are likely sister taxa, there is no evidence for coevolution of *Alcataenia* spp. in these groups.

Alcids had already undergone extensive speciation in allopa-

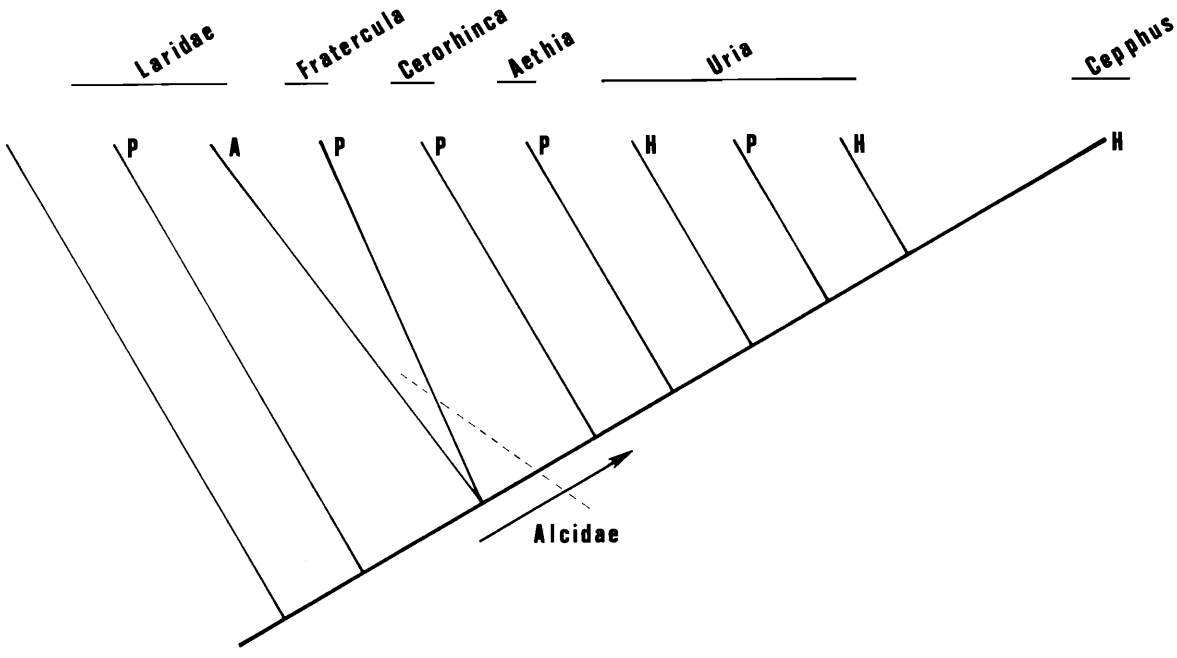


FIG. 10. Cladogram for *Alcataenia* showing host and geographical distribution. Initial colonization of alcids by *Alcataenia* from larids occurred in the late Pliocene (indicated by arrow). P, Pacific endemic; A, Atlantic endemic; H, Holarctic.

tric centres in the Pacific and Atlantic before colonization by *Alcataenia* from larids. The long-term isolation of these centres through the mid to late Tertiary is supported by the lack of a definable cestode fauna linking the endemic alcids characteristic of each oceanic basin. The depauperate nature of this cestode fauna (Hoberg 1984*a*) (Table 3) indicates that dilepidids were not typical of alcids through most of the evolutionary history of the host group. The stability in oceanic provinces and pelagic marine communities since the Miocene (McGowan 1974; Cifelli 1976) and the evolution of an associated assemblage of wing-propelled divers in the Pacific (*Cerorhinca, Aethia, Synthliboramphus, Cepphus, Uria,* and others) and Atlantic (*Australca, Pinguinus, Alca, Alle*) (Bédard 1969, 1976; Olson 1985; Strauch 1985) suggests that trophic pathways were present that could have supported life cycles of *Alcataenia* spp. Consequently, the lack of a well-developed cestode fauna in alcids can be explained in terms of colonization rather than intermittent extinction of parasites within a coevolved assemblage.

A pattern of sequential colonization among ecologically similar hosts dominated the early development of *Alcataenia*. Host switching is postulated to have occurred in ecotone situations: (*i*) from scolopacids to larids (initially terrestrial and estuarine); (*ii*) among larids (estuarine to marine); and (*iii*) from larids to alcids (into pelagic communities).

Alcataenia spp. likely utilize a broad array of pelagic zooplankton as intermediate hosts. Shimazu (1975) reported cysticercoids of *A. larina* and *A. armillaris* from euphausiids (*Thysanoessa inermis*, (Krøyer)) in the North Pacific Ocean. These and other crustaceans are occasionally important prey for many species of seabirds (Ainley and Sanger 1979; Hunt, Burgeson, and Sanger 1981). Thus the possibility of colonization is dependent on guild associations and the degree of overlap in food habits of potential hosts. Successful switching among avian hosts in pelagic ecosystems is rare as indicated by the sporadic distributions of *Alcataenia*. However the potential for colonization is great, judging from the range of incidental hosts reported for some species of helminths (Hoberg 1984*a*, 1984*b*, 1984*c*, 1984*d*, 1984*e*).

The most plesiomorphic species of *Alcataenia* are host-specific parasites of pelagic larids (*A. larina* in *Rissa* and *Larus*) and puffins (*A. fraterculae* in *Fratercula corniculata* and *A. cerorhincae* in *Cerorhinca monocerata*) (Figs. 9, 10) (Hoberg 1984*a*, 1984*c*). These relationships indicate that a minimum temporal limit can be placed on the initial colonization of the alcids. Puffins, *Cerorhinca* spp., are known initially from the Pacific basin in the Miocene, although *Fratercula* occurs initially in the lower Pliocene of the Atlantic. The genus contains two closely related allospecies, *F. corniculata* and *F. arctica*, while a more primitive third species, *F. cirrhata*, is endemic to the Pacific (Johansen 1958; Udvardy 1963; Olson 1985; Strauch 1985) (Figs. 3, 4). Horned puffins are the only known hosts for *A. fraterculae*, while cestodes are generally unknown from the phylogenetically older tufted and common puffins (Hoberg 1984*c*). This distribution is compatible with colonization from larids to horned puffins in the North Pacific during the late Pliocene or early Pleistocene (Fig. 10). It is postulated that host switching occurred subsequent to the vicariance of *F. corniculata* and *F. arctica* after their common ancestor entered the Pacific following the initial opening of Bering Strait as a seaway about 3.0–3.5 million years ago (Repenning *et al.* 1979; Herman and Hopkins 1980; Matthews 1981).

Coevolution of *Alcataenia* within the puffin lineage is discounted because *Cerorhinca* (the most plesiomorphic puffin) (Strauch 1985) is infected with a specific cestode, *A. cerorhincae*, postulated as having been derived from an ancestor similar to *A. larina* or *A. fraterculae* (Figs. 1, 9, 10) (Hoberg 1984*c*).

Alcataenia larina (including *A. l. larina* and *A. l. pacifica*), *A. fraterculae*, and *A. cerorhincae* represent a poorly differentiated group of sibling species in the Holarctic (Hoberg 1984*c*). Host and geographical distributions and morphological attributes of these cestodes support the hypothesis that speciation occurred by peripheral isolation (see Wiley 1981). Isolation of

peripheral subpopulations of an ancestor similar to *A. larina* with a holarctic distribution and subsequent colonization of alcids in the Pacific basin apparently resulted in the development of the *A. larina* complex. The morphological uniformity of the parasites, a polytomy linking *A. l. larina* and *A. fraterculae*, and the parapatric distributions of *A. fraterculae*, *A. l. pacifica*, and *A. cerorhincae* support this contention (Figs. 1, 3, 4) (Hoberg 1984*c*). Speciation of this group could have coincided with the intensified isolation of host populations that would have occurred during one of the early glacial stages, 3.4 or 2.4 million years ago (Herman and Hopkins 1980). Philopatry of hosts would further influence helminths by maintaining isolation following the amelioration of environmental conditions. Evolution of the *A. larina* complex appears to have occurred in conditions of greater environmental stability than those known later in the Pleistocene. Consequently, the morphological conservatism of *A. larina*, *A. fraterculae*, and *A. cerorhincae* is notable (Fig. 1). Postglacial dispersal particularly of puffins in the Pacific (Sealy 1973), has resulted in sympatric or parapatric distributions for the typical hosts of the *A. larina* complex (Figs. 3, 4). However, host specificity within this assemblage has apparently been maintained (Hoberg 1984*c*).

The apomorphic species of *Alcataenia*, from auklets, murres, and guillemots, which evolved later during periods of maximum climatic fluctuation in the Pleistocene are characterized by a high level of homoplasy and alteration in plastic morphological attributes (Table 2, Fig. 1). The evolutionary history of this assemblage during the late Pliocene and Quaternary was directly influenced by the way climate determined the distribution of prey organisms and the suitability of particular geographical localities as nesting sites. Latitudinal shifts in sea surface isotherms, particularly the positions of frontal systems delineating subpolar and polar water, and eustatic changes in sea level (most importantly in Beringia) would have altered the range of habitats available to alcids during stadials and interstadials (see Ruddiman and McIntyre 1976, 1977; Ruddiman *et al.* 1977; Hopkins 1959, 1967, 1971, 1973, 1979, 1982). During glacials, when the Bering-Chukchi platform was emergent (maximum extent, greater than 1000 km in width), it can be assumed that the region was a barrier to dispersal for alcids.

The inception of the first northern hemisphere glacials as early as 3.4 million years ago, and 2.4 million years ago would have intensified latitudinal gradients and influenced distributional patterns of some seabirds (see Herman and Hopkins 1980). However, palaeo-oceanographic evidence presented by Worseley and Herman (1980) and Herman and Hopkins (1980) supports the concept of the Arctic Ocean being free of perennial ice until 700 000 years ago. Through the Pleistocene, significant eustatic changes in sea level (up to 100 m, coinciding with glacial maxima) would have controlled dispersal between the Atlantic and Pacific oceans via the Arctic Ocean and through the Bering Strait (see Hopkins 1967, 1971; Matthews 1981).

The rapid shifts in climate that characterized the Pleistocene may have promoted evolution among *Alcataenia* spp. (see Vrba 1985). During stadials, periods of maximum eustatic reduction in sea level, the north Pacific, particularly the Sea of Okhotsk, Aleutian arc, and Queen Charlotte Islands, and the Arctic Basin, were partitioned into isolated refugia (Udvardy 1963; Warner *et al.* 1982). In these situations, continuity of life cycles for parasites depended on the availability of intermediate hosts that were suitable as prey for alcids. However, once established at a geographic locality, speciation of a particular parasite would have been enhanced by host endemism and philopatry. Site tenacity may explain how birds became isolated in Pleistocene refugia. It also explains maintenance of isolation and apparent inability of some species to colonize otherwise suitable habitats. At the termination of stadials, islands would have sequentially become available as habitat for birds only as sea level rose and the extent of permanent shelf ice decreased (see Hopkins 1982). The Pribilof Islands (St. George and St. Paul) could have been utilized by alcids through the Pleistocene, as they were on the edge of the emergent platform. Islands to the north, St. Matthew, Nunivak, St. Lawrence, and the Diomedes, would only have become available as colony sites coincidental with ameliorating conditions. Megacolonies characteristic of murres, auklets, and other seabirds could only have developed after oceanic conditions became similar to those at present (see Hunt, Burgeson, and Sanger 1981; Hunt, Eppley, and Drury 1981). The distribution of prey organisms may initially have been a primary limitation to recolonization by seabirds and to the continuity of parasite life cycles at some of these localities.

During interstadials the ranges occupied by parasite–host assemblages would expand and the potential for transmission and host switching would be maximized. Conversely, during stadials, vicariance leading to small intensely isolated populations of hosts and parasites with limited gene flow would have promoted speciation within the assemblage. Subsequent colonization and speciation of *Alcataenia* in auklets, murres, and guillemots was influenced by these events.

Alcataenia from puffins are the sister species for *Alcataenia pygmaeus* from auklets (Figs. 1, 9, 10). This dilepidid appears to be limited to *Aethia pygmaea* in a former Pleistocene refugial area in the west central Aleutian Islands (Fig. 2) (Udvardy 1963; Hoberg 1984*b*). Although the recent distributions of the three *Aethia* spp. are sympatric in the western Aleutians and Kurile Islands, it appears likely that each species was confined to a distinct refugial area in the Pleistocene (Udvardy 1963). The limited occurrence of *Alcataenia pygmaeus* is consistent with a host switch to *Aethia* following the isolation and divergence of the whiskered auklet from *Aethia pusilla* and *A. cristatella*. Collections have been inadequate to assess the possible host–parasite relationships of *Ptychoramphus aleuticus* and *Cyclorrhynchus psittacula*.

Three species of cestodes, *Alcataenia armillaris*, *A. meinertzhageni*, and *A. longicervica*, are specific parasites of murres (Hoberg 1984*d*). The former two cestodes have circumpolar distributions, while the latter is endemic to the Pacific (Figs. 6, 7, 10). Based on corresponding geographical ranges of hosts and parasites, it appears that these *Alcataenia* spp. had their origin in the Pacific basin. The precursor for extant species of *Uria* probably entered the North Atlantic via the Arctic in the late Pliocene following the opening of Bering Strait. Murres were likely to have become hosts for *Alcataenia* sp., following a host switch from auklets (Fig. 9) in the Pleistocene, before cladogenesis of *U. aalge* and *U. lomvia*.

The murres are represented by a boreal species, *Uria aalge*, with eight subspecies (Fig. 6), and an Arctic species, *U. lomvia*, with five subspecies (Fig. 7) (Tuck 1960; Udvardy 1963). The genus *Uria* originated in the Pacific basin (Olson 1985) and the initial divergence of *U. aalge* from *U. lomvia* probably occurred when a population of proto-*Uria* became isolated in a high arctic refugium (Sergeant 1951; Storer 1952). The first fossil occurrence of *Uria* sp. (12 000 years ago) in the Atlantic (Olson 1985) indicates that members of the genus had developed a circumpolar distribution at least by the last interglacial,

but more likely at an earlier period. The boreal, circumpolar distribution of common murres suggests that they were widely distributed from the Pacific to the Atlantic before the divergence of *U. lomvia*. Isolation of populations resulting in speciation of *U. lomvia* could have occurred in the Arctic before the onset of major Pleistocene glacials during a period of climatic deterioration in the late Pliocene (see Herman and Hopkins 1980). The rate of evolution among murres is relatively slow; thus a considerable time span may have been required to account for both specific and subspecific differentiation (Storer 1952). Consequently, it is more likely that initial divergence between the murres was late in the Pliocene or early in the Pleistocene, rather than later, and that *U. lomvia* only recently, in the last interglacial, entered the north Pacific. As with other alcids having circumpolar distributions, the development of subspecies of murres coincided with isolation of populations in subarctic and boreal refugia through the Pleistocene.

Alcataenia armillaris, A. longicervica, and *A. meinertzhageni* form a coevolved group in *Uria*. With respect to these species, the phylogenetic tree for *Alcataenia* has two topologies (Figs. 1 and 11).[1] In the most parsimonious tree (CI = 77%), coaccommodation, cospeciation, and host transfer explain the relationships. The holarctic precursor for *U. aalge* and *U. lomvia* would have been a host for *A. armillaris*. Coaccomodation of *A. armillaris* during cladogenesis of *Uria* following vicariance of the host group would have resulted in the circumpolar range of this cestode. *Alcataenia longicervica* then may have developed via cospeciation with *U. aalge* during subspecific divergence of the latter in the Pacific basin. Subsequent isolation of a refugial population of *U. aalge* in the Pacific may have led to the development of *A. meinertzhageni* during the Pleistocene. The holarctic range of the latter species could then be explained by host transfer to other populations of *Uria* spp. through the Arctic basin to the Atlantic during an interstadial. This hypothesis is not well supported as there is no evidence for multiple range extensions by murres through the Arctic basin following the divergence of *U. aalge* and *U. lomvia*. Additionally, host transfer is unlikely, because of the limited vagility of *Alcataenia* in intermediate and final hosts. The potential for widespread interchange of helminths among populations of murres appears limited by philopatry of hosts and endemism of parasites. Among these species of *Alcataenia* it appears that life cycles are maintained primarily on foraging areas adjacent to colonies during the breeding season (Hoberg 1984*a*).

The host and geographical relationships of *A. armillaris, A. longicervica,* and *A. meinertzhageni* provide an alternate hypothesis and support for a slightly less parsimonious cladogram (CI = 74%; Fig. 11). Relative length of the cirrus sac has a postulated reversal in this tree, while relationships of other characters remain unchanged. In this interpretation both *A.*

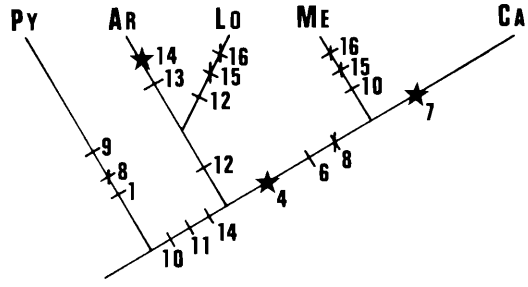


FIG. 11. Alternate topology for cladogram involving *A. armillaris, A. longicervica,* and *A. meinertzhageni* and *Uria* spp. Abbreviations and symbols are defined in caption for Fig. 1.

armillaris and *A. meinertzhageni* attained holarctic ranges in *Uria* and coevolved (coaccomodation) with *U. aalge* and *U. lomvia*. *Alcataenia longicervica* is most closely related to *A. armillaris* and could have been derived in the Pacific by peripheral isolation and cospeciation with a population of *U. aalge* or *U. lomvia* that subspeciated in a Pleistocene refugium. Limited host transfer is compatible with an amphi-Pacific distribution in *Uria* (Figs. 6, 7) and explains the absence of this species in the Arctic basin and Atlantic. The intermediate morphology of *A. longicervica* within this group, and an endemic range in the Pacific suggests, alternatively, that this cestode could have been derived by hybridization of *A. armillaris* and *A. meinertzhageni* with subsequent speciation. In either event, the second cladogram (Fig. 11) appears best supported by subsidiary evidence of host distribution and biogeography.

Alcataenia campylacantha represents the only dilepidid cestode specific to guillemots. Its present geographic distribution parallels that of its hosts (Fig. 5). Complete development to maturity appears to be limited to *Cepphus grylle, C. columba,* and *C. carbo* (Hoberg 1984*a*).

The distributional history of *A. campylacantha* is congruent with that of guillemots. Such a relationship indicates the probability that a *Cepphus* sp. became a host for *A. campylacantha* before the isolation and divergence of the extant species and subspecies of guillemots during the late Pliocene and Pleistocene. *Cepphus* is represented by 3 species and 11 subspecies distributed in the Pacific, Arctic, and Atlantic (Fig. 5). Contrary to Storer (1952) and Udvardy (1963) the genus originated in the north Pacific and only later entered the Atlantic (Olson 1985). *Cepphus carbo* in the Sea of Okhotsk is thought to represent a population isolated in the early Pleistocene, while *C. columba* in the Pacific and *C. grylle* in the Atlantic and Arctic are allospecies of more recent origin (Storer 1952; Udvardy 1963). Dispersal through the Arctic basin before or in the early Pleistocene resulted in a broad geographical distribution for guillemots. Deteriorating climate associated with an undetermined glacial stage probably resulted in elimination of guillemots from the Arctic basin. Populations surviving in the Pacific and Atlantic diverged to become taxonomically recognizable as *C. columba* and *C. grylle*, respectively. Pigeon guillemots have remained confined to the Pacific, although five subspecies have been defined within the amphi-Pacific distribution of the species (Fig. 5). Development of these subspecies reflects additional periods of range contraction, isolation, and divergence during the Pleistocene. Black guillemots are currently represented by six subspecies. Unlike pigeon guillemots, populations of *C. grylle* were able to recolonize the Arctic basin during subsequent interstadials. It is evident that some popula-

[1] In the initial analysis, two competing hypotheses for the phylogeny of *Alcataenia* were produced. In accordance with the tenets of phylogenetic systematics and parsimony (Wiley 1981), the most economical cladogram (Fig. 1; CI = 77%) was considered to be the clearest representation of the present data. However, the empirical evidence from host and geographical relationships did not strongly support the most parsimonious phylogenetic statement. Without rejecting the basis for parsimony analysis, an alternate cladogram differing slightly in tree topology (Fig. 11; CI = 74%) appeared more congruent with the historical biogeography of *Uria* spp. and the geographical ranges of *A. armillaris, A. longicervica,* and *A. meinertzhageni*.

tions survived in isolated Arctic refugia, thus accounting for a high arctic complex of subspecies (*C. g. mandti* and *C. g. ultimus*). Postglacial dispersal accounts for the present distribution of *C. grylle* in regions south of the Bering Strait.

As *Cepphus* is phylogenetically older than *Uria* (Strauch 1985), and *Alcataenia meinertzhageni* and *A. campylacantha* are sister species, the distribution of *Alcataenia* in guillemots is consistent with colonization (Figs. 8–10). Based on the geographical range of *A. campylacantha* and the evolutionary history of guillemots, it is probable that this cestode originated with its host group in the Pacific basin. The holarctic range of *A. campylacantha* in all species of *Cepphus* is consistent with coaccommodation (Brooks 1979*a*).

Recent studies of specimens of *A. campylacantha*, representing populations from the Atlantic, Arctic, and north Pacific oceans, have shown the existence of only minimal morphological variation in cestodes from these allopatric localities (Hoberg 1984*e*) (also observed for *A. armillaris* and *A. meinertzhageni* from murres (see Hoberg 1984*d*)). When considering the degree of specific and subspecific divergence of *Cepphus* spp., the morphological uniformity of this cestode seems notable and provides additional support for a hypothesis of colonization. The retention of *A. campylacantha* over the late evolutionary history of guillemots suggests relative ecological stability with respect to host physiology and also predictability within the parasite–host assemblage. The broad geographical distribution of *A. campylacantha* indicates that environmental conditions and food webs were stable enough to allow completion of the life cycle, at least since the early Pleistocene.

Because of the degree of isolation among extant populations of guillemots, particularly those in the Atlantic, Arctic, and Pacific oceans (Storer 1952), it is unlikely that the distribution of *A. campylacantha* represents a series of recent host transfers. Recent colonization could certainly explain the degree of morphological uniformity of *A. campylacantha*. However, there is likely to be little interchange of birds between colonies, and the vagility of this cestode is probably otherwise limited.

Species of *Alcataenia* have not been described from other genera of alcids. *Alcataenia* sp. indet. was recently reported from *Brachyramphus brevirostris* in Alaska. The large rostellar hooks suggest a relationship with the *Alcataenia larina* – *A. fraterculae* group (Hoberg 1984*e*). Threlfall (1971) found an unidentified species of *Anomotaenia* (=*Alcataenia*?) in *Alle alle* in the North Atlantic. Specific cestodes are not known from *Alca torda* although large collections have been examined (reviewed by Hoberg 1984*a*). The auklets, *Cyclorrhynchus* and *Ptychoramphus*, and the four species of *Synthliboramphus* murrelets have not been studied in sufficient detail. Cestodes in these alcids would also have been derived by colonization; consequently the probability of their occurrence could not be predicted based on this analysis.

The phylogenetic hypotheses presented for *Alcataenia* are consistent with a sequence of colonization of hosts. Although alcids are an ancient group, their cestode fauna is apparently not, having been acquired in the late Pliocene and Pleistocene following diversification of the Alcidae at the generic level in the Miocene. Once particular genera of alcids were colonized, phylogenesis at the level of species and subspecies was generally not accompanied by cospeciation of parasites. A general pattern of colonization, vicariance, and parasite speciation, usually without concomitant host speciation, is postulated (see Brooks 1979*a*). Allopatric speciation of *Alcataenia* was historically constrained by the fluctuating geographic distributions and ecological associations of the host group. Coaccommodation of *Alcataenia* spp. and specific hosts indicates that these parasites were both ecologically and morphologically conservative. Morphological evolution accompanied host switching but was limited after the initial event of colonization. Thus any potential for adaptive radiation was not realized, and morphological evolution of parasites lagged behind continuing diversification of hosts (see Brooks 1985; Brooks *et al.* 1985*b*).

The importance of coevolution, particularly cospeciation in the evolution of helminths, has been indicated in previous studies using phylogenetic methods (Brooks 1977, 1978, 1979*b*; Brooks *et al.* 1981; Platt 1984; Glen and Brooks 1985). Although the role of colonization had been recognized, the dominance of host switching in the evolution of a parasite–host assemblage had not previously been observed (Mitter and Brooks 1983). Additionally, the development of apparently pronounced host specificity in a relatively young assemblage that had developed by colonization would not have been predicted (Price 1980).

The degree of specificity has traditionally been accepted as an indicator of the duration of historical or phylogenetic associations among hosts and parasites (Noble and Noble 1976; Price 1980). Narrow specificity was generally considered to be most pronounced in assemblages of great evolutionary age (Mayr 1957; Manter 1966; Inglis 1971; Price 1980; and others). The phenomenon was often tied to coevolution of an assemblage and as a potential prerequisite for rapid speciation and adaptive radiation within a specific host group (Mayr 1963; Price 1980). Thus, Price (1980) considered euryxenic parasites (generalists) (see Euzet and Combes 1980) to be young colonizers, and stenoxenic and oioxenic parasites (i.e., host specific) to be indicative of relationships within an assemblage in which hosts had accumulated parasites over extended evolutionary time frames. Brooks (1985) indicated that the degree of specificity exhibited by parasite taxa was not necessarily an indicator of the historical duration of parasite–host associations. Previously, Brooks (1979*a*) had suggested that coaccommodation and host specificity be decoupled from long-term coevolution and cospeciation as the latter were not predictive of the former.

The empirical evidence from the present study supports the theoretical concepts developed by Brooks (1979*a*, 1985). The paradigm of narrow host distribution and coevolution is not compatible with the observation of pronounced specificity in an assemblage that originated by recent colonization. Coaccommodation of *Alcataenia* spp. leading to the rapid origin of specificity occurred in the absence of cospeciation.

Subsequent to the initial colonization of the Alcidae, host switching within this group may have been limited by historical constraints related to specificity. *Alcataenia* spp. have not successfully colonized Procellariiformes or other pelagic seabirds that may occur in guild associations with alcids (Ainley and Sanger 1979; Hoberg 1984*a*). Dilepidid cestodes are a dominant family in terrestrial and aquatic birds (Matevosian 1963; Spasskaya and Spasskii 1977, 1978; Schmidt 1986) but are rare components of pelagic communities. Aside from *Alcataenia*, only a single genus of the Dilepidinae is found in pelagic seabirds. In the Antarctic and the Subantarctic, *Parorchites zederi* (Baird, 1853) has a distribution limited to penguins of the genera *Eudyptes* Vieillot, *Pygoscelis* Wagler, and *Aptenodytes* Miller (Fuhrmann 1921; Ippen *et al.* 1981; E. P. Hoberg, unpublished data). Dilepidids are currently not known from pelagic procellariiforms or pelecaniforms. Among charadriiforms, those represented in the Phalaropodinae, Stercorari-

inae, Larinae, Sterninae, Rhynchopinae, and Chionididae are limited to freshwater estuarine and littoral situations. The Hymenolepididae are also broadly represented among avian hosts, but most cycles are aquatic (Rausch 1983; Hoberg 1982). This host distribution indicates that cyclophyllidean cestodes, typical of avian hosts, rarely colonized marine communities.

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